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We started the construction of a system-level simulation package incorporating the ideas of temporal tagging for attentional modulation of neuronal signals into a model of several interacting cortical and subcortical areas using video-camera acquired images. This simulation differs significantly from connectionist models, since the temporal structure of the neural signals plays a crucial role in the coding of attentional state. Thus, we use single neuron models with quasi realistic temporal behavior. In particular, we exclude all models in which the activity of a neuron is measured only by average firing rate. Instead, we assume a spiking mechanism, and that the communication between neurons has to be accomplished by the exchange of potentials.

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Progress Report

October, 1. 1992 - September 30, 1993

Our research has had progress on two different fronts.

I. Design of Simulated Primate Visual System

We started the construction of a system-level simulation package incorporating the ideas of temporal tagging for attentional modulation of neuronal signals into a model of several interacting cortical and subcortical areas using video-camera acquired images. This simulation differs significantly from connectionist models, since the temporal structure of the neural signals plays a crucial role for the coding of attentional state. Thus, we use single neurons models with quasi realistic temporal behavior. In particular, we exclude all models in which the activity of a neuron is measured only by average firing rate. Instead, we assume a spiking mechanism, and that the communication between neurons has to be accomplished by the exchange of action potentials.

The systems-level approach by nature entails that the number of neurons to be simulated will be relatively large. In the interest of obtaining reasonable performance with the available hardware, and also in order to control the number of free parameters of the system, we have had to limit the level of biological realism of the single cell model. Therefore, we decided against a full compartmental modeling scheme, on the assumption that the details of the dendritic arborization are not essential to the behavior of the system as a whole. On the other hand, we have devoted considerable effort to develop a realistic model of the temporal structure of the neural response which goes beyond that of a simple integrate-and-fire neuron. For instance, after a spike has been generated, we simulate the opening of potassium channels which lead to the repolarization of the membrane voltage.

Our evolving simulation package is a tool which we intend to apply to different single neuron models and different anatomical structures. Therefore, for the sake of flexibility, the simulation program was developed with the goal of allowing a maximum of adaptability. We used the object-oriented language C++ which allows the definition of object types (called "classes" in C++) with an inheritance structure. For instance, the simulator employs a number of different neuron classes, all of which are derived from a base neuron class which specifies general neuron characteristics (e.g. they generate spike trains, they receive input via synaptic objects, they have connections -- with weights and propagation delays -- to synapses on other neurons, etc.). However, different derived neuron classes may implement these basic operations in different ways, and they may have additional functionality not possessed by the base class. Some classes of neurons, for instance, generate spikes according to a Poisson process whose time-dependent average rate depends on stimulus parameters and/or attentional state. Other classes integrate their synaptic input, which may include stochastic (noise) contributions, and generate spikes deterministically based only on this input.

The input of the simulator consists of natural images recorded with a video camera, digitized and entered into computer memory. The early stages of visual processing stages, which in biological terms correspond to the retina, the lateral geniculate nucleus (LGN) and layer 4 of cortical area V1, are collectively simulated as a population of orientation selective Gabor filters at different spatial wavelengths. For the sake of performance, we do not simulate individual retinal and LGN cells (as we did in our previous work; see Wörgötter and Koch, 1991, Wörgötter *et al,* 1991). The Gabor filter outputs are used as the input for orientation-selective V1 cells outside layer 4. This input determines the mean spike rates of the V1 cells. The model used for these cells was of the type described above, i.e. they were modeled as Poisson processes with average rate determined by their input. For now, only two orientations (horizontal and vertical) have been used for testing; a larger variety of such filters will be added later.

The access to the simulator is via a graphical user interface. In the enclosed figure, an example of the activity in some of the simulated neural populations is shown, together with the camera image used to generate this activity. The image, shown at the center of the figure, shows a part of a book shelf. On the top are shown the activities of two populations which correspond to the above mentioned Gabor filters of a given spatial wave length (here 3 pixels/cycle). The population on the left consists of cells sensitive to vertical input, the population to the right consists of cells sensitive to horizontal input. The cell activity, in this case corresponding to the average firing rate of a Poisson process, is coded on a color scale where cooler colors correspond to lower activity. When the Poisson process of a specific cell generates an event, the color of this cell is set to red and the cell sends a spike to its postsynaptic partners. Note the differences in activity due to the different orientations of edges in the original image. Such differences are also visible in the next stage, shown in the two lower images. They show the activity in the neural populations to which the Gabor filter cells represented above them project. In this case, the color shows the simulated intracellular voltage of the respective cell, lower (more negative) values being represented by cooler colors. Again, action potentials are shown as red pixels.

We are currently working toward the integration into our system of the V4 representation and the saliency map, so that we may begin to attack the central question of this work regarding the possible biophysical/neuronal basis for selective visual attention.

II. Temporal Tagging in Single Cortical Cells

Let me remind you of the key ideas. In 1990, Francis Crick and I proposed that the action of attention at the neuronal level is two-fold. Firstly, attention <u>tags</u> or <u>labels</u> the output of individual neurons (in that sense, an "attended signal" carries the same information as an "un-attended signal", plus an additional label). The second action of attention is to activate competition among neurons. In the un-attended state, nearby objects in visual space excite different but neighbouring neurons in cortex. Directing one's attention to one of the objects will "label" the neurons in V1 responding to this object and will also activate competition in V4 and IT among neurons responding to the two objects. In this competition, the "labeled" or "tagged" object will now win out, suppressing the response of the neuron to the non-attended object. This theory explains the seminal experiment of Moran and Desimone on the effect of attention in V4 or IT neurons.

How should this tagging be implemented at the level of neurons? Furthermore, how can this "tagging" or "labeling" be de-modulated at the level of V4 or IT. We suggested two possibilities, compatible with our detailed knowledge of the biophysics of cortical cells. One mechanism assumes that the action of attention at the level of V1 is to impart a small oscillatory modulation (in the 40 Hz neighborhood) to neurons responding to objects within the "attentional searchlight." Neurons in primary visual cortex respond to visual stimuli with a Poisson distributed spike train with an appropriate, stimulus-dependent mean firing rate. The firing rate of neurons whose receptive fields overlap with the "focus of attention" is modulated with a periodic function in the 40 Hz range, such that their mean firing rate is identical to the mean firing rate of neurons in "non-attended" areas. This modulation is detected by inhibitory interneurons (interneurons selectively responding to frequency-modulated inputs have been described by R. Llinas and co-workers in 1991) in V4 and is used to suppress the response of V4 cells associated with non-attended visual stimuli. Using very simple single-cell models, we obtain quantitative agreement with Moran and Desimone's (1985) experiments (coming out in *Vision Research*).

A second mechanism we investigated assumes that the cross-correlation among neurons in V1 is modulated by attention. While neurons responding to non-attended objects are assumed to fire in an independent Poisson manner, neurons responding to an "attended object" fire in a temporally synchronized manner; in other words, the cross-correlation among them is increased. Because the firing pattern of individual neurons is random with the same mean rates in both the attended and the non-attended cases, it will not be possible to pick up this subtle "tagging" using single-unit recordings. Interneurons in V4 respond stronger to the synchronized than to the de-synchronized input from V1 and inhibit the response to the non-attended object.

Dr. Tangney

Productivity Report

October, 1. 1992 - September 30, 1993

Principal Investigator: Christof Koch

Contract Grant Titles: California Institute of Technology

A. Publications in peer-reviewed professional journals and refereed book chapters:

Books:

Large -Scale Neuronal Theories of the Brain, C. Koch and J. Davis, eds., MIT Press, in press.

Journals:

Crick, F. and Koch, C. The problem of consciousness. *Scientific American,* **267(3):** 153-159, 1992.

Koch, C. and Schuster, H. A simple network showing burst synchronization without frequency-locking. *Neural Computation* , **4:** 211-223, 1992.

Koch, C. Computational approaches to cognition: the bottom-up view. *Current Opinion in Neurobiology*, **3:** 203-208, 1993.

Softky, W.R. and Koch, C. The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSP's. *Journal of Neuroscience.* **13:** 334-350, 1993.

Refereed book chapters:

Schuster, H. and Koch, C.. Burst synchronization without frequency-locking in a completeley solvable network model. In: *Advances in Neural Information Processing Systems 4*, Moody, J.E., Hanson, S.J. and Lippman, R., eds., pp. 117-124, Morgan Kaufmann, San Mateo, 1992.

B. Number of additional researchers working with the Principal Investigator

Faculty: Christof Koch, PhD, Associate Professor
Ernst Niebur, PhD, Senior Research Fellow
Bartlet Mel, PhD, Senior Research Fellow

Postdocs: William Softky, PhD, Research Fellow

Graduate Students:

Mike Harville, CNS graduate student

C. Professional honors.

None